

ECOLOGICAL RELEASE AND ECOLOGICAL FLEXIBILITY IN HABITAT USE AND FORAGING OF AN INSULAR AVIFAUNA

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The species-poor conditions on islands (MacArthur and Wilson 1963, 1967; MacArthur 1972) are often accompanied by a number of differences in the ecology of insular populations, relative to the ecology of the same species in the mainland source population. Schoener (1965) referred to the broadening of one or more ecological parameters of a population on an island as ecological release. In such release the island population may occupy a wider range of elevations (Diamond 1970a), or more vegetation types (Diamond 1970a, Terborgh and Faaborg 1973, Yeaton and Cody 1974) than mainland counterparts; or may forage with a different, usually broader, range of positions and activities (Cody and Cody 1972, MacArthur et al. 1972, Yeaton and Cody 1974).

The ecological changes are generally explicitly or implicitly attributed to the rarefied competitive environment on the islands, especially in the absence of close taxonomic or ecological relatives, as is implied in the term "release" (Schoener 1965, Cody 1974). However, ecological differences are not always found, even when depauperate insular conditions clearly occur (Diamond 1970b, 1973, 1975; Morse 1971; Simberloff 1974). Furthermore, the ecological change need not be a niche expansion but simply a shift from one pattern of activities to another of equivalent or lesser breadth.

Taxa and guilds have been found to differ in both colonization ability and extent of ecological differences between insular and mainland populations (Morse 1971, 1977; Terborgh et al. 1978). Especially if the good colonists are also ecological generalists (Diamond 1975), insular differences in the ecology of a population may be a response to different available habitats on the island (Power 1976), rather than altered competitive interactions with the other insular populations. Evolutionary processes may, of course, produce similar habitat-related changes in the ecology of insular populations of highly specialized species, but probably over a much longer time period.

STUDY SITE AND METHODS

Gull Island is a small (0.95 km²) island, 3 km offshore from the coast of Witless Bay, Avalon Peninsula, Newfoundland. It supports a depauperate passerine avifauna, relative to adjacent coastal areas, with species richness of about 60% that of South Head, Witless Bay

(Haycock 1973, Vassallo and Rice 1981). To determine the form and extent of the ecological differences between South Head and Gull Island, we examined the habitat use and foraging of four passerine species present in one or both sites. At least two kinds of differences may exist. Differences between sites may reflect differences in habitats available to the species, or they could be cases of ecological release, with the insular population expanding into habitats or foraging areas used on the mainland by populations of species missing on the island. We tried to separate these two evolutionarily different factors when interpreting differences between our populations.

Because of the clear difference in competitive environment, and several comparable studies of foraging in parids (Gibb 1954, Dixon 1961, Smith 1967, Sturman 1968, Krebs et al. 1972, Partridge 1976, Alerstam and Ulfstrand 1977, Morse 1978), we compared attributes of the foraging of Boreal (*Parus hudsonicus*) and Black-capped chickadee (*P. atricapillus*) populations at South Head to the foraging of Boreal Chickadees on Gull Island. The Black-capped Chickadee was absent on the island (Vassallo and Rice 1981). This seemed a particularly clear opportunity for evaluation of the relative importance of resource shifts vs ecological release in insular ecology.

We studied habitat use of Northern Waterthrushes (*Seiurus noveboracensis*), Fox Sparrows (*Passerella iliaca*), Boreal and Black-capped chickadees. The differences in competitive regimes of the insular populations of Northern Waterthrushes and Fox Sparrows were not as obvious as the absence of the congener of the Boreal Chickadee. Golden-crowned Kinglets (*Regulus satrapa*), Northern Parula (*Parula americana*) and Wilson's warblers (*Wilsonia pusilla*) were present at South Head and absent from Gull Island, as were Dark-eyed Juncos (*Junco hyemalis*), White-throated (*Zonotrichia albicollis*), Swamp (*Melospiza georgiana*), and Savannah sparrows (*Passerculus sandwichensis*) present at South Head.

Habitat measures.—The location and general description of the study areas are presented in Vassallo and Rice (1981). During regular morning censuses, singing perches of individuals of the four species were recorded, as were foraging sites for the chickadees. The census records were used to assure that only one plot per individual was included in the habitat measurements (James 1971). Individual plots were measured according to the procedure described in James (1971) and James and Shugart (1970). Tree species and diameter at breast height of each tree (dbh > 2.4 cm) within a circle of 0.04 ha were recorded. Shrub density was determined by counting all shrubs encountered on two arm-width transects at right angles to each other, crossing the center of the plot and covering 33.5 m². Shrubs were identified to species when recorded. An ocular tube (James and Shugart 1970) was used to take 20 + or - readings for canopy and ground cover within each plot. Presence or absence of open water (stream or pond) was recorded at each plot for the Northern Waterthrush samples. Other details were as in James and Shugart (1970).

The number of 0.04-ha samples taken per bird species per site depended on the habitat variability. Additional samples per population were included until consecutive estimates of tree density per plot differed by fewer than 25 trees (James and Shugart 1970). We took six plots for the Gull Island Fox Sparrow population, eight for the Gull Island Boreal Chickadee and nine for the South Head Black-capped Chickadee populations, and seven for all other cases.

A balanced stratified random sampling procedure was used for each species at each site. The stratified design was chosen to insure that samples were drawn equally from each section of both the island and mainland study areas. On Gull Island the presence of numerous Common Puffins (*Fratercula arctica*) reduced the availability of grassy areas for passerines. Therefore, meadows were not included in habitat analyses of either site. Otherwise, when samples were pooled across species, the sampling procedure gave representative samples of all habitats available at each site.

Habitat analyses.—We examined two questions with our habitat analyses. Were there differences in habitat use between mainland and island populations of the bird species? If so, are the “niche shifts” responses to differing habitat characteristics of the two areas, or are they responses to differences in the species composition of the avian communities of the two sites?

The tree or shrub data were converted into proportional occurrences per plot by tree species and diameter breast height. Tree and shrub data matrices were then constructed, rows being tree, shrub or dbh category and columns being the 51 plots. An arcsin transformation was performed on all the proportions (Sokal and Rohlf 1969), and the principal components of each matrix were extracted (Cooley and Lohnes 1971, James 1971). The factor scores for each plot represented the location of each plot on the ecological continua represented by several components. Because the components are orthogonal, a *t*-test was performed on each component to compare the factor scores of all Gull Island plots to the scores of all South Head plots. When the *t*-test was significant, Gull Island and South Head differed in the occurrence of the habitats ordinated along the gradient being considered. When the *t*-test was not significant, the habitat gradient was considered to be comparably represented at both sites.

For factors where the two sites were not different in the first analysis, a *t*-test of the factor scores of island and South Head plots tested whether the species being tested used equivalent parts of the habitat gradient. For habitats differentially represented at the two sites, an additional test was required. A simple *t*-test of factor scores would test for differences in habitat use between populations, but could not differentiate ecological release from responses of the island population to habitat characteristics different from the mainland. The mean and standard deviation of each population were calculated, and the individual factor scores were normalized by conversion to *z*-scores. *T*-tests of the *z*-scores by species then tested whether or not each species was using the same relative position on the habitat gradient at each site, whereas the initial *t*-test had tested whether the populations were occupying the same absolute position on the gradient.

\log_{10} of total tree and shrub densities were compared for each species with a *t*-test and a test for equality of variance (Sokal and Rohlf 1969) to look at island-mainland differences in the preference for, and breadth of, vegetation densities. Canopy and ground cover counts were compared with a Kruskal-Wallis test (Sokal and Rohlf 1969). Means and 95% confidence intervals for maximum tree heights were compared to determine overlap of habitats used by the populations, and tests of equality of variances were done to compare niche breadth between insular and mainland populations.

Foraging activities of chickadees.—Foraging activity was recorded as the frequency of use of different microhabitat positions, using the stopwatch and tape recorded procedure of Cody (1974). Six height classes were used—0.03 m (litter & ground shrubbery), 0.3–1.5 m (low shrub layer), 1.5–3.0 m, 3.0–6.1 m, >6.1 m. Three classes of vegetation were used (1) live deciduous vegetation, (2) live conifer vegetation and (3) nongreen (dead or dying leaves and needles) vegetation and dead trees or limbs. Conifers were subdivided into trunk, center, middle, and periphery, after MacArthur (1958). Data recorded were cumulative seconds an individual spent in each category.

For each of the foraging positions of the chickadees, three comparisons were made. Within populations, data collected from 1–20 June were compared to those collected from 21 June–21 July. For each period, foraging locations of Gull Island and South Head Boreal Chickadees were compared, and locations of Boreal Chickadees at South Head were compared to those of Black-capped Chickadees. Finally, the data were pooled, despite seasonal changes, to examine the most robust differences between the populations. In all cases, the *G*-test for independence of occurrence of discrete events was used (Sokal and Rohlf 1969).

RESULTS

Tree use between sites.—The first two components emphasized structural characteristics of the habitats. Component one was bipolar, ordinating sites from those with predominately small trees with dense, low foliage (mostly balsam fir), to areas supporting predominately trees of large dbh, where dead trees and dense canopy vegetation were common. The second component ordinated plots by increasing density of trees with densest foliage at intermediate layers of the forest, usually white spruce (Table 1). Three other components ordinated plots by increasing densities of tree species, emphasizing respectively, second growth deciduous trees such as mountain ash and mountain maple, black spruce and white birch. Because recent studies have indicated that taxonomic composition, as well as structural characteristics of the vegetation can affect bird species occurrences (Rice et al. 1981, Wiens and Rotenberry 1981), all five components were investigated to insure that subtle patterns of habitat use were not overlooked.

TABLE 1
VARIABLE WEIGHTS FOR VARIMAX ROTATED PRINCIPAL COMPONENTS OF THE TREE COMPOSITION AND STRUCTURE DATA FOR GULL ISLAND AND SOUTH HEAD PLOTS

Variable	Principal component weights				
	PC	1	2	3	4
Trees 2.5–7.6 cm dbh	–0.805	–0.482	0.072	0.208	–0.043
Trees 7.6–12.7 cm dbh	–0.064	0.803	–0.333	–0.076	0.091
Trees 12.7–17.8 cm dbh	0.617	0.583	–0.143	–0.009	–0.066
Trees 17.8–25.4 cm dbh	0.870	0.050	–0.026	–0.107	0.132
Trees 25.4–30.0 cm dbh	0.641	–0.214	0.102	–0.166	–0.097
Trees 30.0 cm dbh	0.553	–0.343	0.320	–0.346	0.106
Balsam fir (<i>Abies balsamea</i>)	–0.831	0.124	–0.300	–0.080	–0.324
Dead trees	0.812	–0.035	–0.046	–0.395	0.115
White spruce (<i>Picea glauca</i>)	–0.023	0.680	0.031	–0.034	–0.128
White birch (<i>Betula papyrifera</i>)	0.395	–0.365	–0.301	0.060	0.903
Black spruce (<i>Picea mariana</i>)	–0.134	–0.157	–0.016	0.855	0.047
Mountain ash (<i>Sorbus americana</i>)	0.173	–0.343	0.574	0.029	0.228
Mountain alder (<i>Alnus crispa</i>)	–0.176	–0.000	0.027	0.848	–0.081
Mountain maple (<i>Acer spicatum</i>)	0.160	–0.252	0.827	–0.250	–0.079
Juneberry (<i>Amelanchier bartramiana</i>)	–0.111	0.160	0.714	0.159	–0.362
Percent variance explained	30.9	18.7	9.8	8.8	6.5

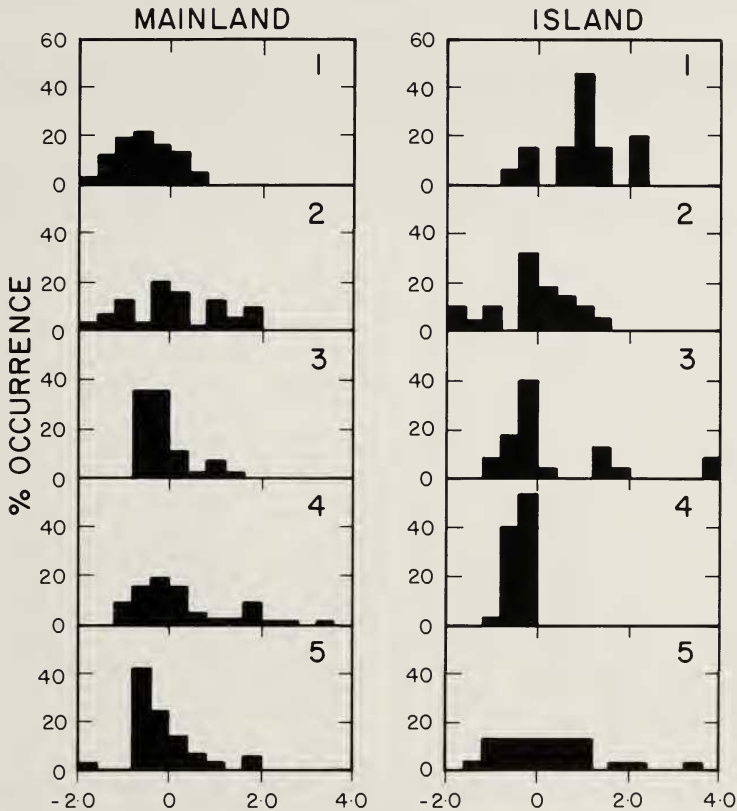


FIG. 1. Histograms of occurrences of plots from South Head (mainland plots) and Gull Island (island plots) on the five principal components from analysis of tree species composition and vegetation structure; x axis is principal component score. Numbers 1-5 refer to specific components.

Plots of habitats characterized by components 2, 3 and 5 were equally represented at Gull Island and South Head ($t = 0.95, 1.32$ and 1.46 [for components 2, 3 and 5, respectively]; $df = 49$; $P > 0.05$; Fig. 1). On component 1, South Head plots had significantly lower factor scores than did Gull Island plots, indicating denser understory vegetation, more balsam fir, and fewer large or dead trees ($t = 7.71, df = 49, P < 0.001$). Scores on component 4 were also significantly different ($t = 3.33, df = 49, P < 0.01$). Fig. 1 illustrates that although most plots at both sites supported low to intermediate densities of black spruce and/or mountain alder, at South Head a few plots had exceptionally high densities of these trees.

TABLE 2
VALUES OF t FOR COMPARISONS OF FACTOR SCORES FROM PRINCIPAL COMPONENT ANALYSES OF TREE AND SHRUB COMPOSITION BETWEEN POPULATIONS OF BIRDS ON SOUTH HEAD, WITLESS BAY, AND GULL ISLAND, 1977

Factor	Northern Waterthrush	Fox Sparrow	Boreal Chickadee	Boreal Chickadee (S) ^a Black-capped Chickadee (S)
Tree analysis				
1	5.07**	5.55**	1.40	0.291
2	1.08	0.202	2.04	0.373
3	0.237	1.53	0.541	1.26
4	1.51	1.58	3.10*	0.255
5	0.178	0.884	2.14	1.49
Shrub analysis				
1	1.37	2.90*	1.91	0.440
2	1.39	0.975	0.149	0.004
3	1.62	0.541	1.56	0.805
4	0.577	1.51	0.733	0.794
5	1.31	4.20**	0.383	0.985
6	0.851	0.337	0.437	0.234
7	1.37	0.0426	0.778	0.193
df =	12	11	14	13

* $P < 0.05$ (2-tailed t -test).

** $P < 0.01$ (2-tailed t -test).

^a (S) for South Head populations only.

When the habitats on the samples from the four species are compared using these factor scores, several differences are found (Table 2). The Gull Island populations of both the Northern Waterthrush and Fox Sparrow differ significantly from the South Head populations on component 1; the Boreal Chickadee populations differ significantly on component 4. However, the two South Head chickadee populations do not differ in habitat use.

Because all significant differences in factor scores were for habitat attributes that differed between sites, the z -transformations and subsequent tests were necessary to determine what ecological differences existed. For each species the distribution of the populations relative to the available habitats did not differ significantly (Fox Sparrow: $t = 0.86$, $df = 11$, NS; Northern Waterthrush: $t = 1.31$, $df = 12$, NS; Boreal Chickadee: $t = 0.26$, $df = 14$, NS). Thus, the differences in habitat use between South Head and Gull Island populations reflect responses to differences in the range of habitats rather than competitively based ecological displacements.

When total tree densities were compared by t -test, no differences were

TABLE 3
 DESCRIPTIVE STATISTICS AND COMPARISONS BETWEEN POPULATIONS FOR TREE AND SHRUB DENSITIES ON PLOTS USED BY FOUR PASSERINE SPECIES AT SOUTH HEAD, WITLESS BAY, AND GULL ISLAND, 1977

	South Head			Gull Island		
	\bar{x}	\pm	SD	\bar{x}	\pm	SD
Tree density						
Northern Waterthrush	99.9		27.7	90.1		27.6
	0.713 ^a		0.001 ^b	—		—
Fox Sparrow	59.7		10.5	93.9		65.3
	1.18		7.88*	—		—
Boreal Chickadee	124		71.0	100		21.3
	0.531		4.01*	—		—
Black-capped Chickadee	123		39.5	—		—
	1.09		2.10	(compared to South Head Boreal Chickadee)		
Shrub density						
Northern Waterthrush	52.0		16.6	13.6		14.2
	3.06*		0.124	—		—
Fox Sparrow	53.6		12.8	30.7		9.62
	3.11*		0.401	—		—
Boreal Chickadee	46.7		21.5	20.1		12.4
	2.62*		0.820	—		—
Black-capped Chickadee	42.3		13.7	—		—
	2.16		0.564	—		—

^a *t* values for tests of equality of means, unequal variances assumed.

^b Chi-square value for test of homogeneity of two variances.

* $P < 0.05$.

found for any of the species (Table 3). The variances were significantly different for both the Fox Sparrow and Boreal Chickadee, the former more generalized on South Head and the latter more so on Gull Island.

Shrub use between sites.—Because of the significant differences between sites on component 1 of the tree analysis emphasizing understory vegetation, we looked in detail at the shrub composition of the vegetation at the sites. Little systematic structure was apparent in the vegetation at this level, with seven eigenvalues greater than 1.0 in the principal component analysis of the shrub vegetation (Table 4). Components 2 and 4 were bipolar, whereas all others ordinated density variation in one or two shrub species. Sites on Gull Island were distributed differently from those at South Head on components 1, 3 and 5 ($t = 4.18$, $P < 0.001$; $t = 2.15$, $P < 0.05$; $t = 3.18$, $P < 0.02$; respectively, all $df = 49$). Other gradients in shrub composition were equally represented at both localities (Fig. 2).

When positions of the four species on these components were compared,

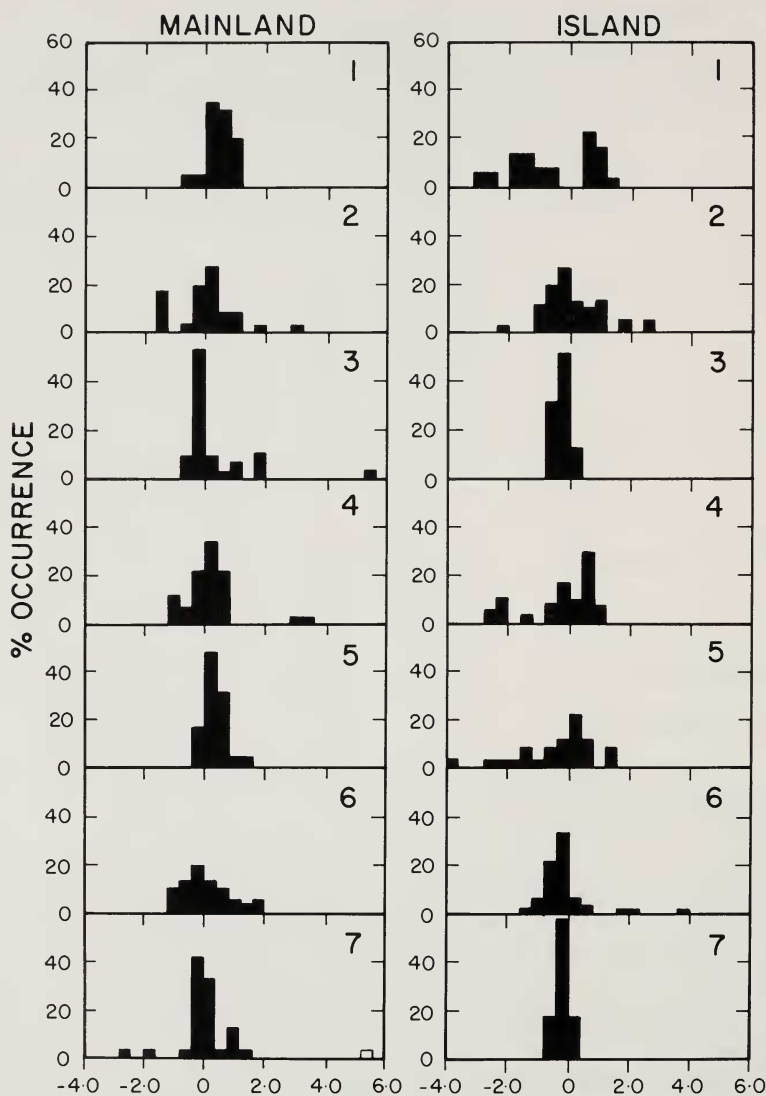


FIG. 2. Histograms of occurrences of plots from South Head and Gull Island on the seven principal components from analysis of shrub composition of the vegetation. Axes and symbols as in Fig. 1.

only the Fox Sparrow populations showed significant differences on components 1 and 5 (Table 2). Because both of these habitat gradients were differentially represented in the two areas, the relative positions of the populations were again tested by analysis of z -scores. No difference be-

TABLE 4
 VARIABLE WEIGHTS FOR VARIMAX ROTATED PRINCIPAL COMPONENTS OF THE SHRUB COMPOSITION DATA FOR GULL ISLAND AND SOUTH HEAD PLOTS

Variable	Principal component weights						
	PC 1	2	3	4	5	6	7
Balsam fir	0.244	0.880	-0.043	-0.020	0.031	0.056	0.060
Mountain alder	0.490	-0.327	0.030	0.434	0.464	-0.147	0.134
Dead shrubs	0.010	0.099	0.011	-0.676	0.381	-0.288	-0.173
Wild raisin (<i>Viburnum cassinoides</i>)	0.368	-0.605	0.116	0.102	0.094	0.386	0.001
Juneberry	-0.023	-0.030	0.070	0.048	0.085	0.874	0.053
White birch	0.079	0.046	0.016	-0.005	-0.860	-0.120	-0.058
Mountain ash	-0.855	-0.039	0.052	0.007	0.160	0.021	-0.045
White spruce	0.312	0.254	-0.184	-0.606	-0.093	0.155	-0.211
Black spruce	0.139	-0.075	0.837	0.027	0.029	-0.119	0.109
Mountain maple	-0.601	-0.270	-0.235	0.157	-0.443	-0.053	-0.047
Pin cherry (<i>Prunus pensylvanica</i>)	0.094	0.075	-0.025	0.102	0.089	0.068	0.874
Mountain holly (<i>Nemopanthus mucronata</i>)	-0.115	-0.025	0.789	0.002	-0.011	0.254	-0.127
Mixed other uncommon species	0.163	0.238	-0.117	0.626	0.205	0.068	-0.448
Percent variance explained	16.2	14.6	10.8	9.1	8.4	7.9	7.7

TABLE 5
KRUSKAL-WALLIS H-VALUES FROM COMPARISONS OF CANOPY AND GROUND COVER
COUNTS AT SOUTH HEAD AND GULL ISLAND FOR FOUR PASSERINE SPECIES

Species	Canopy cover	Ground cover
Northern Waterthrush	1.99	9.49*
Fox Sparrow	7.44*	3.48
Boreal Chickadee	0.07	1.05
Boreal Chickadee (S) ^a vs Black-capped Chickadee	0.48	3.69

* $P < 0.01$, 2-tailed comparison.

^a (S) is South Head only.

tween populations was found for component 1 ($t = 0.79$, $df = 11$), but on component 5 a barely significant difference appeared ($t = 2.32$, $df = 11$, $0.04 < P < 0.05$). On Gull Island the Fox Sparrow was using areas with relatively high white birch densities, whereas on South Head it was using areas with relatively low densities of this tree. This may represent a shift in the relative position of the Fox Sparrow in an insular avian community.

When total shrub densities are compared, all three species occupy habitats with significantly higher shrub densities on South Head than on Gull

TABLE 6
SUMMARY OF COMPARISONS OF ATTRIBUTES OF HABITATS OF FOUR PASSERINE SPECIES
ON SOUTH HEAD, WITLESS BAY, AND GULL ISLAND

	Fox Sparrow ^a	Northern Waterthrush ^a	Boreal Chickadee ^a	Boreal Chickadee ^b vs Black-capped Chickadee
Tree density	- ^c	-	-	-
Tree density variance	+ ^d	-	+	-
Tree composition	+	+	+	-
Shrub density	+	+	+	-
Shrub density variance	-	-	-	-
Shrub composition	+	-	-	-
Canopy cover	+	-	-	-
Ground cover	-	+	-	-
Maximum tree height	-	-	-	-
Maximum tree height variance	+	-	-	-
Presence of water		+		

^a Comparison of South Head and Gull Island populations.

^b Comparison of the two South Head populations.

^c Minus means that the comparison was not significant.

^d Plus means that the test was significant. Specific tests are presented in Tables 2, 3 and 5, and the text.

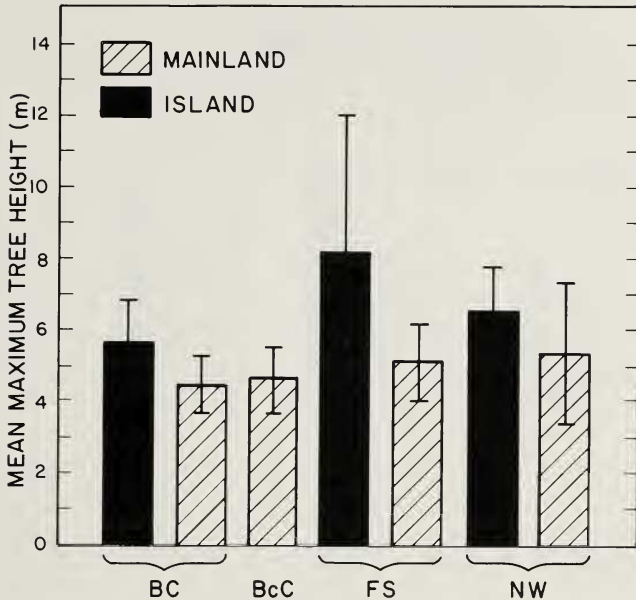


FIG. 3. Means and two standard deviations for maximum tree height on plots of each of the populations studied. BC = Boreal Chickadee, BcC = Black-capped Chickadee, FS = Fox Sparrow, NW = Northern Waterthrush, Mainland = South Head, Island = Gull Island.

Island (Table 3). However, the shrub density on South Head is greater than on Gull Island by an amount comparable to the between-population differences. Again, these differences reflect differences in available habitat rather than competitive interactions between species. The Boreal and Black-capped chickadee habitats did not differ in shrub composition or density at South Head.

Other habitat attributes.—The canopy cover differed between Gull Island and South Head only on plots of the Fox Sparrow (Table 5); the areas used on Gull Island were significantly more open. Only the Northern Waterthrush occupied areas with significantly greater ground cover on South Head than on Gull Island. No populations differed in mean canopy height, but the variance of canopy height on the Fox Sparrow sample from Gull Island was significantly greater than on South Head ($\chi^2 = 5.94$, $df = 1$, $P < 0.025$, Fig. 3). Finally, at South Head all seven waterthrush plots had open water present, as is characteristic of the species (Bent 1953), whereas, on Gull Island only 1 of 7 plots had open water present. Table 6 summarizes all the habitat analyses between South Head and Gull Island populations.

Chickadee foraging.—Differences in foraging location were found be-

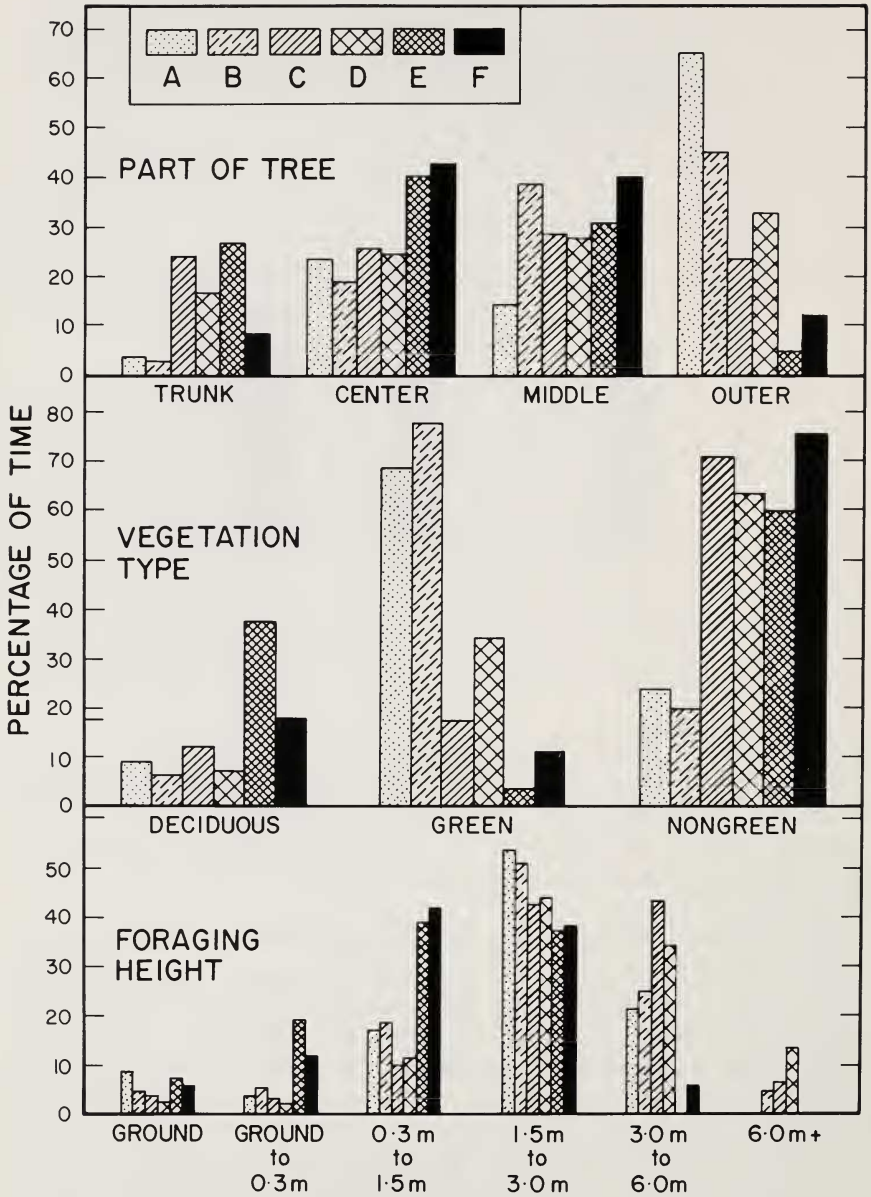


FIG. 4. Proportion of time spent foraging in each category by each chickadee population during early and late seasonal intervals. A = South Head Boreal Chickadees until June 20; B = South Head Boreal Chickadees after June 20; C = Gull Island Boreal Chickadees until June 20; D = Gull Island Boreal Chickadees after June 20; E = South Head Black-capped Chickadees until June 20; F = South Head Black-capped Chickadees after June 20.

TABLE 7
VALUES OF STATISTICS FOR G-TESTS OF THE FORAGING POSITION DATA IN FIG. 3, FOR
EARLY VS LATE COMPARISONS OF EACH CHICKADEE POPULATION, AND BETWEEN
POPULATIONS WITHIN EACH PERIOD

Early vs late	Boreal Chickadee		Black-capped Chickadee	
	South Head	Gull Island	South Head	
Foraging height	110.4	1838.6	47.9	
Vegetation type	14.3	1885.8	76.7	
Part of tree	135.7	36.5	71.0	
Total seconds	2632	3732	3422	
	Boreal Chickadee		Boreal Chickadee vs Black-capped Chickadee	
	South Head vs Gull Island		South Head	
	Early	Late	Early	Late
Between populations				
Foraging height	310.0	2159.3	297.7	877.1
Vegetation type	687.7	837.9	525.2	5989.9
Part of tree	396.5	37.5	260.8	757.3

All $P < 0.005$.

tween months for each chickadee sample, between Gull Island and South Head Boreal Chickadee populations, and between the two species at South Head (Table 7, Fig. 4). From early June to late June—early July each population tended to increase use of high parts of trees. Foraging decreased on deciduous trees and increased on green vegetation for all groups. Both Boreal Chickadee populations decreased use of nongreen vegetation, whereas blackcaps increased use of those areas. Island Boreal Chickadees tended to forage more towards the outer ends of branches and less on trunks later in the season, whereas South Head Boreal Chickadees decreased use of both of those areas, and increased the use of middle sections of trees.

Despite the extensive seasonal changes, significant differences were consistently present between populations. Boreal Chickadees on Gull Island foraged significantly higher in trees than either South Head group, and South Head Boreal Chickadees foraged significantly higher than did Black-capped Chickadees. Taller trees on Gull Island might account for some of this difference (Fig. 3). Both Gull Island Boreal and Black-capped chickadees foraged mainly in nongreen vegetation, whereas South Head Boreal Chickadees foraged largely in green vegetation. On South Head the two species partitioned the trees, with Boreal Chickadees using outer sections and blackcaps using inner sections. On Gull Island the Boreal Chickadees used all sections of the trees fairly evenly.

DISCUSSION

For each of the species examined, some differences in habitat use between mainland and island populations were found: the Fox Sparrow populations differed most, then the Northern Waterthrushes, and the Boreal Chickadees least. With one exception the differences in habitat use are reflections of differences in available habitat. Aside from the increase in use of white birch by Gull Island Fox Sparrows, explanations of mainland-island differences do not require additional consideration of changes in competitive interactions among species. Other insular differences from mainland populations also reflect ecological flexibility: insular Fox Sparrows increased variance in tree densities and heights used, insular Boreal Chickadees used a wider range of tree densities and waterthrushes resided in areas lacking open water.

Partitioning of foraging microhabitat by the two species of chickadees was found at South Head, consistent with the findings of previous workers on foraging of *Parus* species (Smith 1967, Sturman 1968, Partridge 1976, Morse 1978). Boreal Chickadees on Gull Island increased their use of inner parts of trees, bare branches and deciduous vegetation, areas used on South Head by Black-capped Chickadees. Corresponding to this increase in foraging microhabitat breadth, the island Boreal Chickadee density equalled or exceeded the combined density of both chickadees on South Head (Vassallo and Rice 1981).

Seasonally, similar trends were seen in the foraging activities of all populations. Perhaps these similar trends are responses to changing food availability as the season progressed. The flexibility in foraging location necessary to exploit seasonally varying food supplies may account for the greater ecological release found in the chickadees' foraging microhabitats than in the macrohabitat-use patterns of the species considered. Further, the two South Head chickadee populations showed several differences in seasonal foraging trends, such as the decreased use of nongreen vegetation by Boreal Chickadees, and the increased use of the same areas by black-caps. These trends are consistent with the interpretation that competitive factors greatly affect foraging activities (Cody 1974).

Our findings are consistent with the literature documenting ecological shifts between mainland and island populations of many species, as cited in the introduction. Consistent with theory (Schoener 1965, MacArthur and Wilson 1967, many others) many changes, such as increased variance in several measures, indicate niche expansion of insular populations. However, for other ecological differences, including changes in species composition of habitats used and foraging heights, invoking changes in competition as explanation for the differences is unnecessary.

A number of studies have argued that species which are particularly

good colonists are often ecological generalists (Simberloff and Wilson 1969, 1970; Diamond 1975; Terborgh et al. 1978). Our findings are consistent with that proposal. For species showing ecological flexibility we found competition may not be necessary to explain even large differences between mainland and insular populations. If available island habitats differ from adjacent mainland areas, their use by populations of a particular species could differ greatly. Nonetheless, the populations in question could be filling the same relative role or guild in both communities, and be optimizing use of available habitat. However, a species occupying habitats similar in absolute properties could in fact be playing very different roles in the insular and mainland communities.

In our study, it appears that microhabitat foraging positions are more likely to show direct effects from changes in competitive pressures, although it was not possible to document the extent of insular differences in available prey. Our conclusion is inferred from the increased use by insular Boreal Chickadees of areas used on South Head by Black-capped Chickadees. Such flexibility in foraging location has been found in other studies of parids (Krebs et al. 1972, Partridge 1976). Flexibility in microhabitat use should be common to enable foraging activities to respond to seasonal variation in resources. Consequently, for insular populations of birds, microhabitats used for foraging activities may be preadapted to show a faster and greater response to changing competitive regimes than do macrohabitat preferences. Careful comparisons of both habitats and foraging resources available, as well as those used, are necessary to distinguish the effects of competition and simple ecological flexibility on insular community dynamics.

SUMMARY

Aspects of macrohabitat use by Fox Sparrows (*Passerella iliaca*), Northern Waterthrushes (*Seiurus noveboracensis*) and Boreal Chickadees (*Parus hudsonicus*) differ between insular Newfoundland and coastal populations of each species. The differences generally reflected changes in the ranges of available habitats between localities, rather than responses to differing competitive environments. Foraging locations of coastal and insular Boreal Chickadee populations were also compared. Differences were found—the Boreal Chickadee expanded the breadth of its foraging activities to include areas used on the mainland by Black-capped Chickadees (*P. atricapillus*), a species absent on the island. Seasonal differences were also found in chickadee foraging behavior at both sites. Niche partitioning between the two mainland species of chickadees was accomplished via differences in foraging position rather than macrohabitat differences.

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